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WHY BONELLI'S EAGLES HUNT IN PAIR : AN ASSESSMENT OF INDIVIDUAL AND PAIRED HUNTING SUCCESSES[1]

MILIND G. WATVE, NIRANJAN R. SANT AND VIJAY JOSHI[2]

(*With a text-figure*)

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The hunting strategies and hunting successes of a breeding pair of Bonelli's Eagles were studied over five breeding seasons. Active hunting singly was found to be the most efficient method of hunting followed by active hunting in pair. The sit and wait methods were less efficient. In spite of active hunting in pair being significantly less efficient than hunting singly, the eagles spent much time soaring and hunting together. The possible explanations for this behaviour are discussed in this paper.

INTRODUCTION

The Bonelli's Eagle (*Hieraaetus fasciatus*) is a, slender built, medium sized resident eagle inhabiting lightly wooded hill ranges. It hunts either by a quick dash from cover (referred in this paper as the "sit and wait" method) or scans the hillsides while soaring and makes a stoop (the "active search" method). The breeding pair remains together even outside the breeding season and both the partners are often seen soaring and hunting together (Brown and Amadon 1968).

The hunting strategies of a breeding pair of Bonelli's eagles were observed over five breeding seasons to see whether hunting together is more beneficial than hunting singly. There could be following potential advantages of hunting in pair: (1) increase in search efficiency; (2) increase in killing efficiency; (3) the pair can kill larger prey than individuals; (4) protecting the kill from rivals; (5) reduction in handling time; (6) greater net energy gain.

It is also possible that one of the eagles is a cheater and takes advantage of the hunting skills of the other (Packer and Ruttan 1988). All of the above possibilities are discussed in the light of field data.

MATERIALS AND METHODS

A pair of Bonelli's eagles (*Hieraaetus fasciatus*) is resident in a hill range along the north-west boundaries of Pune city. Their nest was located on a *Dalbergia* sp. tree at about 15 metres height. The foraging behaviour of the pair was observed over five breeding seasons beginning from 1985-86. The nesting period was chosen for observations because the activities were centred around the nest, making observations easier and also there was much variation in the total food requirement during the nesting period. Out of the five seasons more than 70% of our observations came from the 1986-87 and 1988-89 seasons. Observations were restricted

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[2]Life Research Foundation, 10, Pranav Society, 1000/6C, Navi Peth, Pune 411 030.

to week-ends and holidays. By placing three observers at a time along the crest line of the hill stretch, it was possible to keep the eagles in sight for 50 to 90% of the times during a day.

The following data were recorded:

1. The breeding success of the pair in 5 consecutive seasons: The success or failure to rear the nestlings to the fledgling stage was recorded for each year.

2. Time spent in active hunting and food gathered: The time spent in soaring, hunting attempts and prey handling was included in the active hunting time. The total time spent in active hunting per day and the number of kills brought to the nest were noted. When the eagles soared out of sight for a short time and returned, they were assumed to be hunting actively. However, when they were out of sight for more than 25% of the day, the day's observations were not included in this data.

3. Hunting efficiencies: When the eagles were in sight, the time spent in soaring alone or in pair, as well as the time spent on perch were recorded. The number of hunting attempts and the outcome was noted. Hunting efficiencies, search efficiencies and killing efficiencies were calculated from these data (Table 2).

Results and Discussion

The breeding success of the pair over 5 years was 0.8 fledglings per year (Table 1). This is similar to the success of the European race of Bonelli's eagles (0.8/pair/annum) and larger than the African race (0.5/pair/annum) (Brown and Amadon 1968).

Table 1

Year	No. of eggs laid	No. of nestlings survived
1985-86	?	1
1986-87	2	2
1987-88	2	0
1888-89 (first attempt)	2	0
1988-89 (second attempt)	1?	1
1989-90	2	0

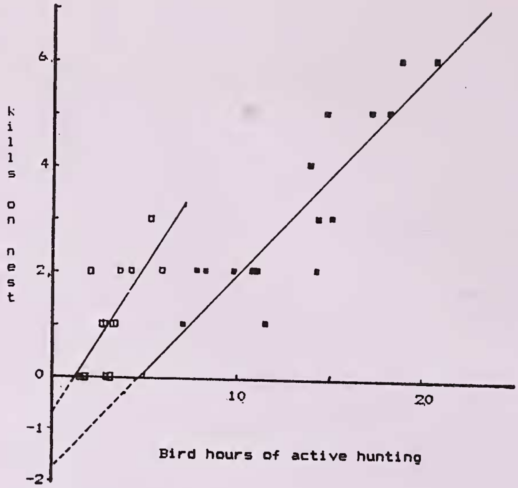

Fig. 1. Number of kills brought to the nest as a function of the time spent in active hunting.
[a] □ days when only the male hunted
r = 0.712 0 slope = Ya - Yp = 0.5437
Y intercept = -0.63054 estimated Kc = 2.196
[b] ■ days when both parents hunted
slope = 0.36032 Y intercept = - 1.6796
estimated Kc = 4.0286 (see equation 1.)

Throughout the five breeding seasons, the male hunted alone during incubation period and fed the female on or near the nest. This practice continued for two weeks after hatching. Between the 12th to 14th day the female joined the male in hunting for part of the day and her contribution increased rapidly during the following week. In the third and fourth week the pair did most of the active hunting together. In the 1986-87 season, when two nestlings successfully fledged, during the 6th to 8th week the eagles spent much time hunting separately in different locations particularly in the afternoon. In other seasons they tended to soar together for most of the time.

The efficiency of active search method was observed to be much higher than the sit and wait method (Table 2). This is consistent with the observation that, when the food requirement of the family was low, the sit and wait method was preferred, but as the food requirement of the family increased, more and more time was spent in active

TABLE 2

Hunting method		Single	Paired
Sit and wait	Hours observed	121	21.05
	no. of attempts per hour (search efficiency)	0.876	1.473
	success/attempt (killing efficiency)	0.198	0.355
	success/hour (hunting efficiency)	0.174	0.523 (0.261/bird hour)
Active search	Soaring hours observed	53.19	49.10
	no. of attempts per hour (search efficiency)	3.1	2.65
	success/attempt (killing efficiency)	0.33	0.43
	success/hour (hunting efficiency)	1.02	1.14 ** (0.507/bird hour)
No. of observed cases of failure to protect the kill		3 out of 54	0 out of 56
Mean handling time per kill (min.)		9.35	10.02

We test the null hypothesis that the efficiency of paired hunting = twice the efficiency of single hunting, by the likelihood ratio test.
** Null hypothesis rejected, efficiency of paired hunting less than twice that of single hunting.

hunting (Fig. 1). If we assume a fixed limit 'T' to the maximum number of hours available for hunting in a day, this time could have been divided into sit and wait and active hunting. We can therefore write the mean number of kills in a day (K) as,

K = ta*Ya + (T-ta)*Yp where, ta = time spent in active hunting
Ya = efficiency of active hunting
Yp = efficiency of sit and wait

An estimate of K was difficult to obtain in the field since the eagles could be consuming a few kills when out of sight. An accurate record of the number of kills brought to the nest was however maintained and therefore we can write,

Kn + Kc = ta*Ya + (T-ta) * Yp
where, Kn = no. of kills brought to the nest
Kc = mean no. of kills consumed away from the nest or,
Kn = ta (Ya-Yp) + TYp - Kc ——— (eqn. 1).

Since Ya > Yp (Table 2), a straight line with positive slope is expected when we plot the number of kills brought to the nest against the time spent in active hunting (Fig. 1). An estimate of Kc can then be obtained from the intercept.

In the active search method, as opposed to sit and wait method, by pairing the hunting success did not double (Table 2). The search efficiency of the pair in fact seemed to be less than that of individuals. This might be because when two birds were flying, the probability of alerting the prey was more (Anderson and Norberg 1981). This probably did not apply for sit and wait method where the search efficiency of the pair was observed to be more. The killing efficiency of the pair was better for both the methods but in case of active hunting this did not compensate for the twofold work input and decrease in search efficiency. Thus the eagles did not seem to do better by soaring together. In spite of this, the eagles seemed to prefer soaring together for 35 to 90% of the times in a day's hunt during the 3rd to 7th week of brooding.

The prey species could not be identified every time a kill was observed. From examination of remains of kills and pellets, no appreciable difference could be noted during incubation, when the male hunted alone and during 3rd to 7th week, when most of the hunting was done in pair. Throughout the study period, the majority of prey ranged in size between quails and pigeons. A hornbill kill was found during incubation phase when the male hunted alone. A black naped hare was seen killed by the male alone. Thus there was no convincing evidence that the eagles killed larger prey when hunting together.

On three occasions the eagles lost their kill to either the tawny or the steppe eagles. On all these occasions the eagles were alone. A similar incident has been reported by Dharmakumarsinhji and Lavkumar (1972). On the other hand the pair was seen exchanging a kill in air in presence of three steppe eagles soaring immediately above. Thus apparently the pair was able to protect the kill better when together. The observed data do not show a statistically significant difference in the frequencies of being robbed when hunting singly or together. Assuming robbery to follow Poison distribution we can see that the chances of observing zero robbery are 0.2171, which is fairly high. But even if we assume the pair to be protecting better, the frequency of being robbed was not high enough to justify hunting in pair.

From energy considerations, hunting in pair could be beneficial if the net energy gain per unit time of the pair was more than double that of individuals. The net energy gain per unit time is defined as the energy gain per unit time from successful kills - the energy loss per unit time from unsuccessful attempts. Therefore,

$$Ys\,(Es*Ps*Ks - \{1-Ks*Ps\}\,E's) < \frac{Yd\,(Ed*Pd*Kd - (1-Kd*Pd)\,E'd)}{2}$$

where, Y = search efficiency (no. of attempts per hour)
E = mean energy gain per successful kill
K = killing efficiency (success/attempt)
P = probability of protecting the kill successfully from rivals
E'= energy loss in unsuccessful attempt

the suffix 's' denotes hunting singly and 'd' denotes paired hunting.

With the empirical values (for Ys, Ks, Yd, Kd, Ps, Pd, and with the assumption that Es = Ed and E's = E'd, it can be seen that,

$$3.1*\,(0.92*0.33*E - 0.67*0.92*E') < 2.65*\,(1*0.43*E - 0.57*1*E')/2.$$

This condition will be satisfied only if E' > 0.321 E. This is highly unlikely because with the energy loss in unsuccessful attempts being so high and only one attempt in three (Table 2) being successful, the eagles would hardly get enough for themselves and feeding the nestling would be impossible. Secondly, since they make use of thermal currents for soaring and gravitational force for diving, the energy input is not expected to be very high. This can be seen from the following computations. From Fig. 1a and eq.1 the mean number of kills consumed by the male per day during incubation period can be calculated to be 2.196. The incubating female on an average consumed one kill per day. If the basic metabolic requirement of the male is assumed to be similar, active hunting must have increased the requirement by 1 to 1.5 kills. The male made 3 to 5 kills per day during this period, which would mean about 9 to 15 attempts given the killing efficiency as 0.33. If 9 to 15 attempts increase the food consumption by 1 to 1.5 kills, the E'should not exceed 0.167 times E.

Active hunting in pair, therefore, cannot be explained on time and energy considerations. If the hunting efficiency of an individual is high, no advantage is expected by pairing (Packer and Ruttan 1988). Yet Bonelli's eagles soar together very frequently. If availability of food is not the limiting factor in regulating brood size or breeding success in case of eagles (Meyburg 1974), hunting strategies need not be optimized with respect to time and energy by natural selection. In such a case other factors like strengthening the pair bond or cheating might be more important in determining behaviour.

Throughout the nesting period, the male did the majority of the hunting and the female may be considered to be partially parasitic on the male. During incubation period, when the female was almost totally dependent on the male for food, soaring together was hardly ever observed. In paired hunting the initiative was most often taken by the male and the female followed. However, many times the actual killing was done by the female. On three occasions, after locating the prey, the male stooped first followed by the female; the male missed the target but the female captured it successfully. This could be the reason why the killing efficiency of the pair was more than individuals. When only one nestling was reared, the maximum number of kills made in a day was 7 or 8. With the empirical hunting efficiency of individual hunting as 1.02/hour (Table 2) and assuming 9 to 10 hunting hours a day, the male alone could have gathered enough for the entire family. In spite of this the female joined the male in hunting. Thus neither the female seemed to be dependent on the male throughout the nesting period, nor soaring together was necessary when there was maximum dependence.

These data thus suggest that Bonelli's eagles do not hunt in pair in order to increase the efficiency of hunting. Although the efficiency of paired hunting is significantly low, it probably plays some role in the social behaviour of the eagles as very often they are seen soaring together. Soaring together may be important for strengthening the pair bond, advertisement of the territory or any other factors which could not be quantified during this study.

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